THE TAXONOMIC VALUE OF PORE CHARACTERS IN THE GRASS AND SEDGE RUSTS[1]

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It is only in recent years that the germ-pores of the urediniospores of the rusts have been the objects of critical study by the mycologist. This study has been prompted by the desire to find additional morphological characters of sufficient constancy and clearness for taxonomic purposes.

The first consistent use of urediniospore-pore characters in the description of rust species was made by the senior author of this paper in the second number of the North American Uredineae, issued in 1898 and printed in the Bulletin of the University of Iowa. They had occasionally been incorporated in descriptions prior to this but had not been used with any constancy. The prevailing tendency had been to regard all of the urediniosporic characters as of slight taxonomic value and to place the greater dependency on characters of the teliospores. The recent authors of systematic works on the rusts who have used urediniospore-pores most consistently are Fischer, Holway, Bubak and Grove. None of these authors, however, have incorporated these pore characters in their keys as has been done in the rust part of the North American Flora, the first number of which was issued in 1907.

In no groups of the rusts has the taxonomist's need of sharply distinctive morphological characters been more imperative than in those which have their uredinial and telial stages on grass and sedge hosts. These are included under two genera, *Nigredo* (*Uromyces* in part) and *Dicaeoma* (*Puccinia* in part); the former with one-celled and the latter with two-celled teliospores. There is a growing belief, which has been strengthened by the study of the urediniospore-pores, that there is no essential difference between the two genera and that the presence of more than one cell

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in the teliospore is a racial feature rather than an acceptable morphological basis of separation. When both one- and two-celled teliospores occur together the generic assignment is arbitrary, it being understood that the two-celled spores are to be given preference, even if comparatively few, or if quite absent in part of the sori or on some hosts. The species may still be maintained in two genera for convenience and in conformity with usage. The determination of the species, however generically disposed, on teliosporic characters alone is often a difficult task and sometimes an impossibility, on account of the great similarity of the forms. It has become necessary, therefore, to utilize such other characters as are available and especially those of the urediniospores.

Urediniospores can usually be found in collections of grass and sedge rusts even though no uredinial sori are present. A scraped mount made from a sorus of teliospores will usually contain a few of the other spores even if the collection be made at a season when uredinial production has apparently ceased. There are, however, three species of grass rusts, *Puccinia leptospora, P. Campulosi* and *P. paradoxica,* in none of which have urediniospores been observed. These are rare species represented by single collections only. Teliospores, on the other hand, are by no means an omnipresent spore form of the grass and sedge rusts, They are seldom present in uredinial sori at the optimum growth period of the host, and in many species they are almost entirely wanting throughout the whole season, as in the common rust of blue-grass, *Puccinia epiphylla,* which produces teliospores in North America in alpine or boreal regions only. The urediniospore is, as a rule, the most abundant spore form and its characters are sufficiently constant and distinctive to make it of great value for taxonomic purposes.

The most useful urediniosporic characters are: the form and size of the spore, the color and thickness of the spore wall, its surface sculpturing, and the number and distribution of the germ-pores. Among these the pore characters are perhaps the most valuable. The pores are usually visible in a water mount but it is often better to use a clarifying or staining agent to bring them out distinctly. A small drop of lactic acid mixed with the water in which the spores are mounted, especially if heated to

the boiling point, is very effective, as is also the application of a solution of chloral hydrate and iodine. The latter is particularly serviceable when the spores are fresh and still retain their colored contents. These methods fail, however, in a few species having urediniospores with colorless or thick gelatinized walls. There are five of these species: three, *Puccinia versicolor, P. Boutelouae,* and *P. triarticulata,* in which the pores are evidently scattered but the exact number cannot be made out, and two species, *P. Seymouriana* and *P. Melicae,* in which neither the pore number nor distribution is known.

According to our present knowledge there are 145 species of rusts on grass and sedge hosts in North America having available pore characters; 105 species on grasses and 40 on sedges. The following account of urediniospore-pores is based upon this group of species, which includes those with both one- and two-celled teliospores.

In the grass rusts the urediniospore-pores vary in number with the different species from 2 to 12. In species where the pores are restricted to the equatorial zone the most common number is 3 or 4, and where the pores are scattered, 6 or 8.

In the sedge rusts the range of variation, 1 to 5, is much smaller, five pores being the largest number known. The two-pored condition is most common and the one-pored condition, found in two species only, is rare.

The extent of variation in number of pores in a single species is usually small. A variation of four, as from 8 to 12, is the extreme. Many species have a variation of two, as from 2 to 4, 4 to 6, etc., or of one, as from 2 to 3 or 3 to 4, and in many the pore number is fixed.

The real significance of the pore number from the physiological standpoint is not known and no theory to account for the presence or importance of more than one pore in each spore has been put forth. The pore number and distribution are no doubt associated in some way with the development of the species and possibly bear a physiological relation to the host. Their absolute hereditary constancy has never been proven. An apparent physiological modification in the pore number and distribution is known in *Pucinia*

vexans, a common rust of the prairies on species of *Bouteloua.* In addition to the normal thin-walled urediniospores this species produces a resting or amphisporic form of urediniospores. These amphispores have a thick, dark-colored wall and are easily mistaken for teliospores of *Uromyces.* They show their urediniosporic nature, however, by the production of a germ-tube instead of a promycelium, and by their ability to reinfect the same host. The normal urediniospores of this species have eight scattered pores, while the amphispores have four equatorial pores (Fig. 1, *b* and *c*). An explanation of the difference in number and position of the pores in the active and resting urediniospores should give a valuable insight into the evolution of this stage of the rusts.

It is sometimes more difficult to ascertain the disposition of the the pores than their number. This is especially true in a globoid spore, as it is hard to be certain that it is properly orientated, but an ellipsoid or oblong spore will naturally lie upon the proper surface for convenient examination. Three general types of distribution are recognized: scattered, equatorial, extraequatorial.

The term scattered pores does not imply that the pores are without a definite arrangement. They are practically equidistant from each other over the cell surface in the typical scattered-pore condition (Fig. 1, *a, b* and *d*).

If the pores are equatorial, they more or less approximate the equator of the spore and are placed at about equal distances apart (Fig. 1, *e, f, g,* and *h*).

The extraequatorial group may be conveniently subdivided into pores superequatorial, and pores subequatorial. Like the equatorial-pored condition these are zonal arrangements when more than one pore is present. The zone may be slightly above or below the equator (Fig. 1, *j*), considerably above, near the apex (Fig. 1, *i*), or considerably below, near the hilum (Fig. 1, *k* and *l*). Two pores is the constant number for all of the extra-equatorial-pored species except those with pores near the hilum. One species, a grass form, *Puc. Sporoboli,* has three pores arranged in a zone around the hilum, while two species, both sedge forms on species of *Carex,* each have a single pore near the hilum.

The scattered- and equatorial-pored conditions are present in

about equal numbers in the rusts under consideration. There are at present known 63 species with scattered pores and 67 with equatorial pores. Fifteen species have extraequatorial pores, eleven

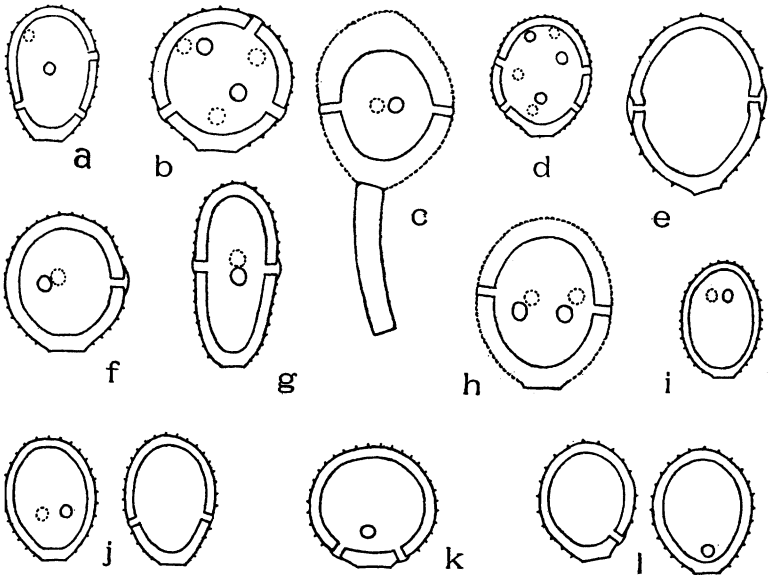

Fig. 1, *a, b, d–l,* urediniospores and *c,* amphispore, all from North American collections: *a, Uromyces Poae,* 5 scattered pores; *b, c, Puccinia vexans,* 8 scattered pores and 4 equatorial pores; *d, P. epiphylla,* 10 scattered pores; *e, P. Cenchri,* 2 equatorial pores; *f, P. Urticae,* 3 equatorial pores; *g, P. poculiformis,* 4 equatorial pores; *h, P. eslavensis,* 6 equatorial pores; *i, P. Caricis-Asteris,* 2 superequatorial pores; *j, P. Caricis-Strictae,* 2 subequatorial pores; *k, P. Sporoboli,* 3 basal pores; *l, Uromyces uniporulus,* 1 basal pore. All spores magnified 625 diameters.

of which are super- and four subequatorial. Expressed in percentage, the different divisions stand as follows: pores equatorial 46.2 per cent.; pores scattered 43.5 per cent.; pores superequatorial 7.6 per cent.; pores subequatorial 2.7 per cent.

None of the grass rusts has superequatorial pores and but a single species has subequatorial pores. All of the remaining species, therefore, in which the pores are known, belong to the scattered- or equatorial-pored groups, 63 species in the former group and 42 in the later.

Among the sedge rusts the scattered-pored condition is very uncommon, being found in but a single species, *i. e., Puc. karelica.*

The equatorial-pored condition is most common here and is present in 25 species, while eleven species have superequatorial pores and three have subequatorial pores.

The practical importance of a thorough understanding of the pore characters of the urediniospores of the grass and sedge rusts, apart from the possible clues of relationship and phylogeny that may be derived from it, lies in the application of the knowledge to the identification of incomplete material. In many cases collections that are of considerable importance in mapping the range of a species or in determining its validity are represented by a few fragments of leaves that the taxonomist is unable to place and the rust material may be scanty and wholly or chiefly in the uredinial stage. The too common practice of gathering a few infected leaves without infloresence or fruit supplemented by the failure to properly label the collection in the field leads to many errors in the naming of hosts which the uredinologist is sometimes able to rectify through the proper identification of the parasite. If a rust in question on an unidentified grass-like fragment of leaf has scattered urediniospore-pores or a greater number than five the assumption is that the host is a grass since but a single sedge rust has scattered pores and none has more than five. If the pores are superequatorial, the host is most certainly a sedge.

With the few broad bases of separation afforded by the pore characters and with the other supplementary characters of the urediniospores, it is often possible to determine the species of rust from urediniosporic material alone, which is a far cry from the situation prevailing not many years ago when grass and sedge rusts, especially the latter, were considered the most difficult of all the rusts to determine, and utterly hopeless when only urediniospores were present.

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